CONTRIBUTIONS TO OUR KNOWLEDGE OF AMERICAN CARBONIFEROUS FLORAS

IX. Some Petrified Seeds from Iowa

ELLEN M. KERN
AND HENRY N. ANDREWS

This is a third contribution that has accrued from our study of the coal-ball collections of Mr. Frederick O. Thompson of Des Moines, Iowa, the two previous accounts (Parts VII and VIII of "American Carboniferous Floras") giving a detailed description of the origin of the specimens. All of the fossils described herewith were found in coal balls from the Urbandale mine located immediately west of Des Moines.

During the decades that have elapsed since the time of Brongniart's ('81) foundational memoir on the silicified seeds from Saint-Etienne a rather vast assemblage of fossil seeds have been described from Paleozoic deposits. Although relatively few have been found attached to the plants that bore them they have contributed very appreciably to our knowledge of the three great groups of Carboniferous seed-bearing plants—the Pteridospermeae, Cordaitales, and Lycopodiales. Comprehensive summaries of the many genera and species are included in the works of Seward ('17) and Arnold ('38).

With the exception of *Lepidocarpon,* few structurally preserved seeds have been recorded from the Carboniferous of North America, most of the known species having been found in European deposits. There is now some evidence to indicate that certain areas of the Pennsylvanian forests of Illinois were predominantly pteridophytic, and since much of the American coal-ball work to date has been confined to collections from that state the apparent paucity of seeds is accounted for at least in part. It should be added, however, that only a few of the coal mines of even Illinois have been subjected to intense study, and it will certainly be some years before we arrive at a clear picture of the composition of the ancient forests that are represented in the coal balls. In a previous discussion a brief contrast was drawn between the coal-ball flora of Illinois and that of Iowa, seeds being present in Iowa in much greater numbers. Although there are at least seven species of seeds, exclusive of *Lepidocarpon,* in our present collection we have selected for description only the better-preserved ones.

Conostoma Williamson, 1877.
Conostoma oblongum Williamson.

Only one specimen of this species has turned up in our Urbandale collection thus far, and since it has been described with considerable precision by Oliver and Salisbury ('11) from the Lower Coal Measures of Lancashire a detailed account is not warranted here. More recently it has been reported by Krick ('32) from the

upper part of the Carbondale group at Harrisburg, Illinois.

The Iowa record given here is based on a specimen that was exposed in longitudinal section, although the cut had been made slightly beyond the median plane. The seed (pl. 18, fig. 2) measures nearly 4.5 mm. long by 2 mm. in diameter and shows no pronounced tapering toward either end. The apical portion of the nucellus (fig. 3) is quite well preserved, showing the distinctive generic features of the pollen chamber in which two pollen grains may be noted. The integument is lobed at the micropylar end, somewhat more distinctly so than in the previously described specimens.

Conostoma oblongum is described by Oliver and Salisbury as being platyspermic although in their own words it is "only trifling in amount," and their figures adequately bear this out. In view of the general wide range in cross-sectional shape of the petrified Carboniferous seeds there can be little doubt that more fundamental structural features, such as the organization of the pollen chamber and the nature of the integument, are of greater significance. In other words, Seward's classification of the Paleozoic seeds into three groups, the Lagenostomales, Trigonocarpales, and Cardiocarpales, is certainly preferable to the older system based on cross-sectional shape.

Aside from Krick's citation of *Conostoma oblongum* in an Illinois coal ball, the only previously known American species are those described by Graham ('34). His well-executed figures of *C. platyspermum* leave no doubt as to the generic identity of this fossil, and although it is very close to *C. oblongum* its segregation as a distinct species seems justified.

Rhabdospermum Seward, 1917.

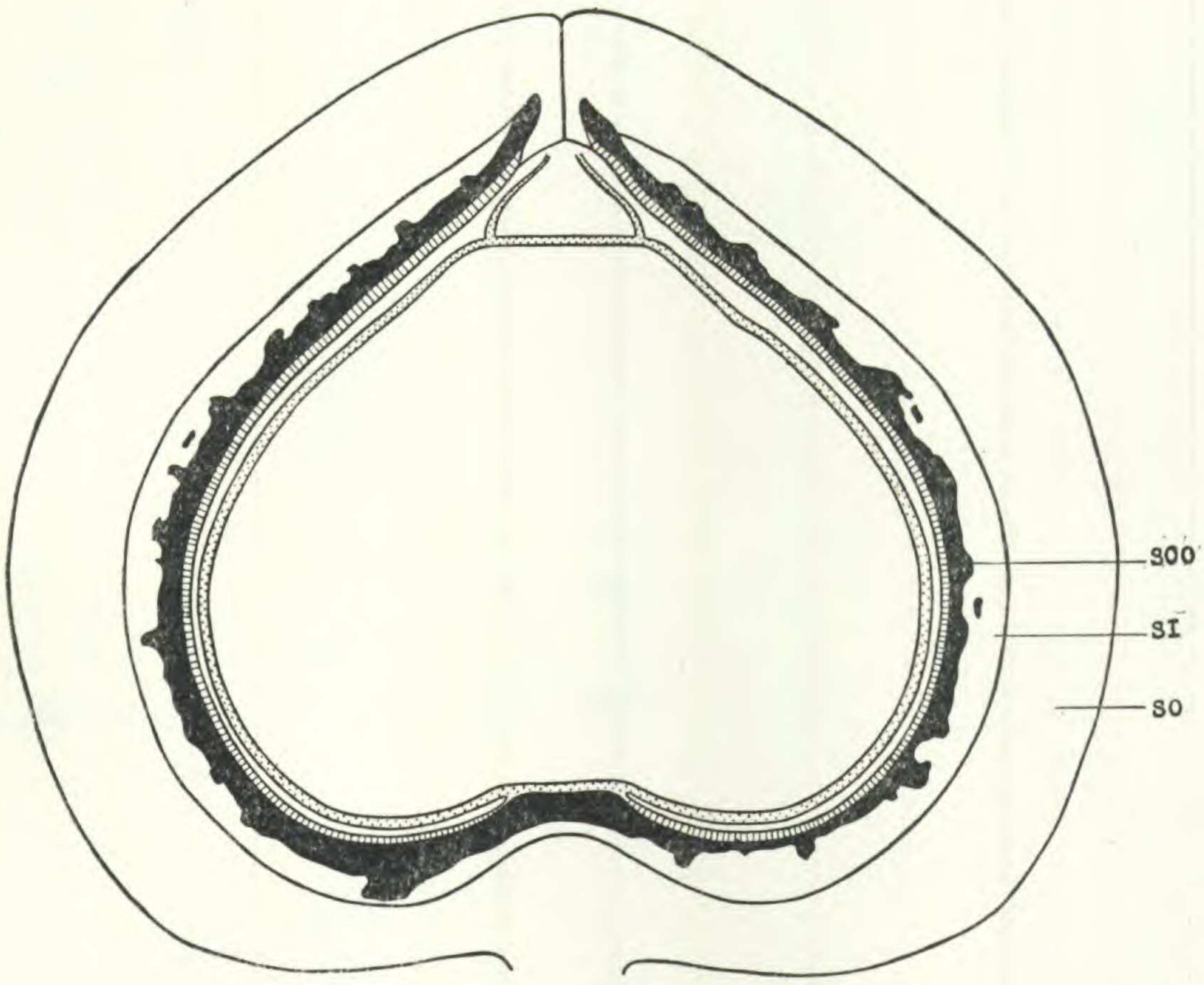
Rhabdospermum spinatum Andrews, sp. nov.

The fossil seeds, preserved as both petrifactions and impressions, that are of Cordaitean affinities already compose a striking assemblage displaying considerable variation in size, form, and anatomy. The fact that the vast majority of these seeds (included in the Cardiocarpales as classified by Seward, '17, pp. 332-356) have been described from European Carboniferous deposits by no means implies their restriction to that region. Cordaitean stem, root, and foliage remains are of frequent occurrence in the Illinois and Iowa coal balls. Although the present description is based on a single, incomplete seed, it seems worth recording inasmuch as it presents characters that distinguish it from any previously described species.

The seed is heart-shaped in longitudinal section and relatively large, measuring 15 mm. broad by 12 mm. long. The integument, which is composed of four clearly defined tissues, is especially well preserved. Following the nomenclature used by most previous workers, the outer two tissues will be referred to as the *sarcotesta* and the inner, more sclerotic two, as the *sclerotesta* (text-figs. 1, 2).

The outer sarcotesta, which is appreciably thicker than the three inner zones

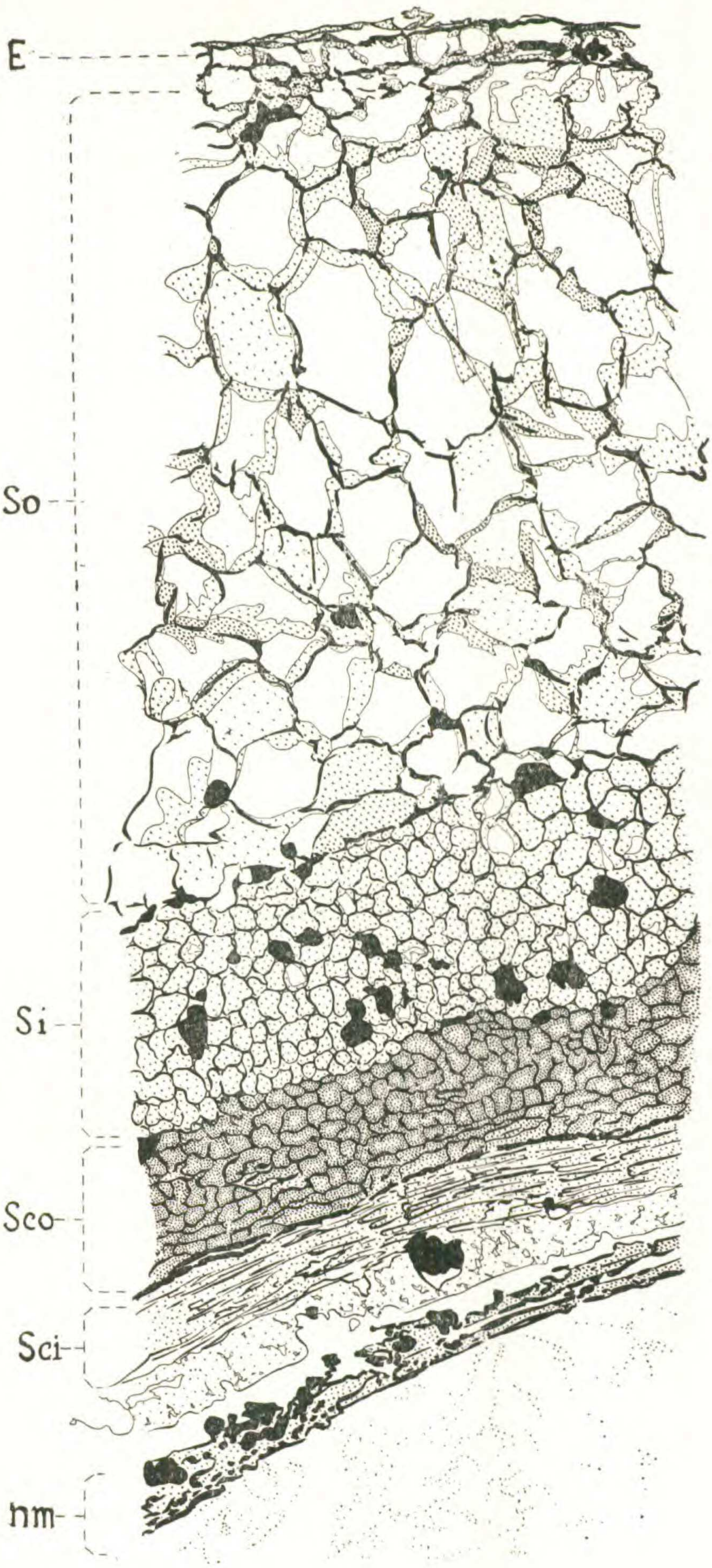
combined, is composed of large, relatively thin-walled cells averaging about 200μ[1] in diameter (text-fig. 2, So). In life this must have been of a fleshy texture, probably comparable with that of the outer coat of a *Cycas circinalis* seed. This outer sarcotesta is bounded by an epidermis of much smaller, vertically elongated cells averaging about 115μ x 70μ. The cells of the inner sarcotesta (Si) are nearly isodiametric, like those of the outer tissue, although much smaller, averaging 50μ.



Text-fig. 1. *Rhabdospermum spinatum.* Diagram of the seed shown in median longitudinal section, with pollen chamber restored: SO, outer sarcotesta; SI, inner sarcotesta; SCO, outer sclerotesta.

The sclerotesta appears as a conspicuous dark brown band, the color being due partly to the cellular contents. Like the sarcotesta, it is composed of two clearly defined tissues (text-fig. 2, Sco, Sci), although relatively much thinner and not as readily distinguishable at lower magnifications (pl. 18, fig. 1). The outer component (Sco) consists of cells similar in shape to those of the inner sarcotesta

[1] All cell measurements of these integumentary tissues have been taken from the plane of the nearly median longitudinal section shown in pl. 18, fig. 1.



Text-fig. 2

Rhabdospermum spinatum

Cellular detail taken from the equatorial region: E, epidermis; So, outer sarcotesta; Si, inner sarcotesta; Sco, outer sclerotesta; Sci, inner sclerotesta; nm, remnants of nucellus and megaspore membrane.

although thicker-walled. The most conspicuous feature of this tissue is the irregularly shaped spines projecting into the inner sarcotesta, and it is in recognition of this character that the specific name has been chosen. The inner sclerotesta consists of cells that are very poorly preserved but which apparently were elongated in the plane of the longitudinal axis.

The remnants of the nucellus are clearly attached to a raised cushion at the base of the seed although it otherwise appears to be quite free from the integument. It should be noted that, since the innermost tissues of the sclerotesta and of the adjoining nucellar tissue are not perfectly preserved, it is not certain whether the two were originally in organic connection. Yet the space between them is so uniform as to imply that it is natural rather than due to shrinkage or decay.

Very little remains of the nucellar tissue. At its apex, however, it appears to have developed in the form of a broad conical pollen chamber (pl. 18, fig. 1, text-fig. 1). Although little more than the cuticularized remains of the epidermal cells are left, the form of the integument in this region also suggests such a terminal structure of the nucellus. Thus the internal conical cavity presents a distinct contrast to the flattened one in *Rhabdospermum cyclocaryon* (Ad. Brongn.) Seward (Brongniart, '81, pl. XII, fig. 1).

Affinities:—The affinities of this seed appear to lie with the closely related genera *Cardiocarpus*, *Rhabdospermum* and *Mitrospermum* of the Cardiocarpales. The last two of these genera are distinguished from *Cardiocarpus* chiefly in the way that the vascular strands originate from the main bundle. In *Cardiocarpus* the outer (lower) bundles depart from the main vascular axis before the latter reaches the sclerotesta, while in *Rhabdospermum* and *Mitrospermum* they are given off from the sclerotesta region and recurve back into the outer portion of the integument (cf. Seward, '17, figs. 500B and 501E).

As stated above, the only available specimen of this seed was exposed on a previously cut slab from Mr. Thompson's collection. The fact that the initial cut was apparently made directly through the central vascular strand leading up through the base of the seed makes it impossible to determine whether the integument branches departed from the main bundle before or after reaching the sclerotesta. The one observable integumentary strand passes out between the outer and inner sarcotesta, more closely comparable with the position of the bundles in *Rhabdospermum* (Seward, '17, fig. 501E) than in *Cardiocarpus* (Seward, '17, fig. 500B). Moreover, the strikingly distinct integumentary tissues of *Rhabdospermum spinatum* compare very closely with *Rhabdospermum cyclocaryon* (see Brongniart, '81, pl. XII, fig. 3). The spinose nature of the sclerotesta of the new seed sets it apart from *R. cyclocaryon* or the apparently closely related *Mitrospermum compressum* (Will.) A. Arber.

Diagnosis:—Rhabdospermum spinatum: platyspermic seed 15 mm. broad x 12 mm. long; integument composed of four tissues: an outer conspicuously thick sarcotesta, inner sarcotesta, outer spinose sclerotesta, and inner sclerotesta of longitudinally elongate cells; pollen chamber shaped like an inverted shallow teacup.

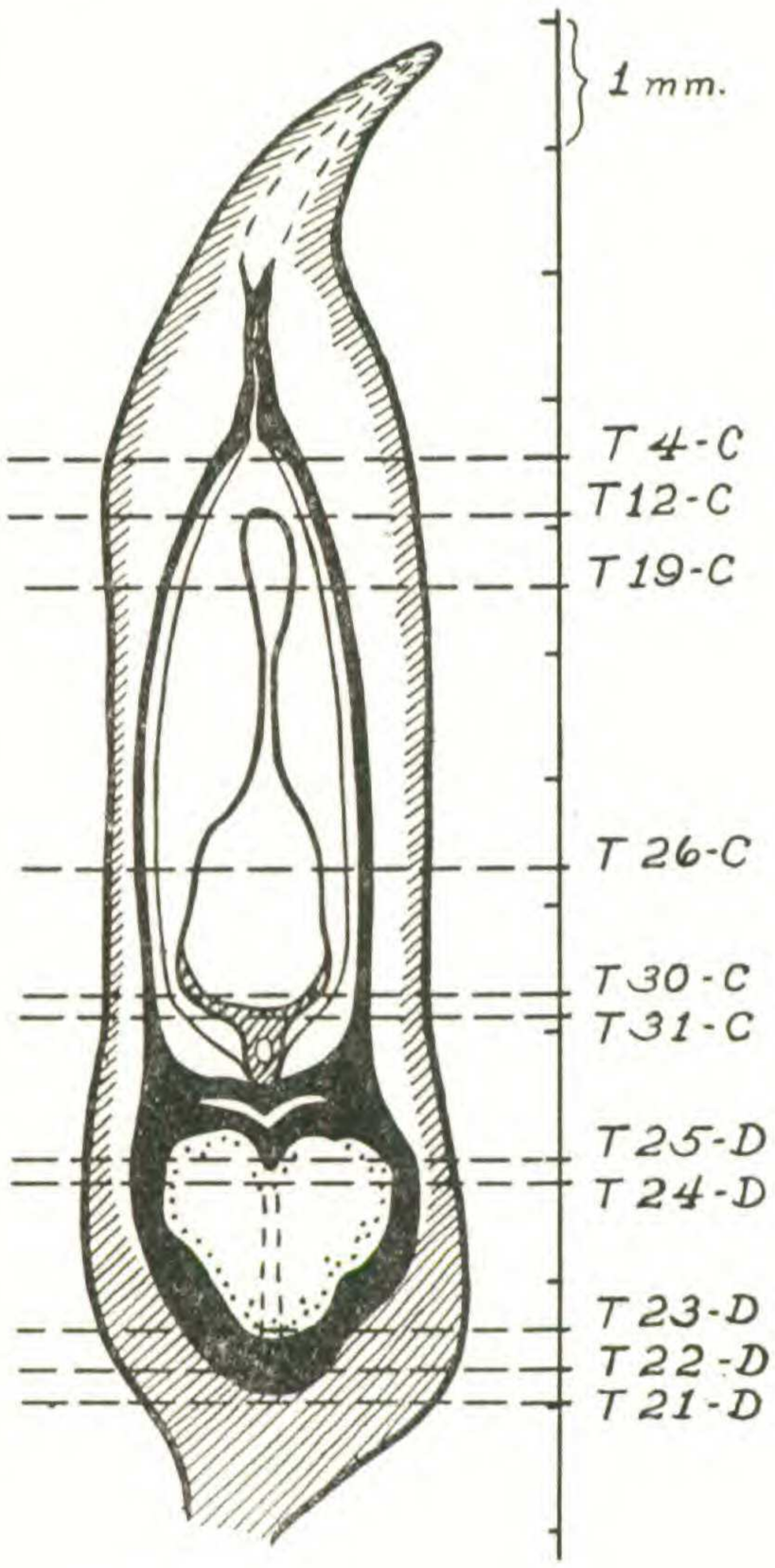
Locality: Urbandale Coal Mine, Des Moines, Iowa.

Horizon: Des Moines Series, Pennsylvanian.

Type specimen: No. WCB493, Henry Shaw School of Botany paleobotanical collections.

Kamaraspermum Leeanum Kern, gen. et sp. nov.

One of the Urbandale coal-balls received from Mr. Thompson contained a dozen or more specimens of a seed which, because of its highly distinctive structure, is designated herewith as a new species, *Kamaraspermum Leeanum*[2].



Text-fig. 3. *Kamaraspermum Leeanum.*

Diagrammatic median longitudinal section along the minor axis (from seed A, peel 475-T 21). Horizontal broken lines indicate corresponding positions of transverse sections through seeds C and D (see text-fig. 5). The seed tissues are indicated as follows:

Epidermis—outer black line.
Outer sclerotic integument—striped area.
Outer parenchymatous integument—white area.
Inner sclerotic integument—black.
Inner parenchymatous integument — white area delimited by inner sclerotic integument and thin black line.
Nucellus and megaspore membrane.
Probable course of vascular strand—broken line through basal chamber.
Parenchymatous cells of basal chamber—black dots.

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[2] The prefix *Kamara* is from the Greek, meaning a chamber or room with an arched covering. The species is named for Mr. Arthur F. Lee, Chief Engineer of the Binkley Coal Company's Pyramid Mine, Pinckneyville, Illinois. Mr. Lee's most cordial cooperation during the past six years has been an indispensable aid in our coal ball collecting.

In spite of some pyritization the seeds are quite well preserved, and the orientation of two of them has allowed the preparation of satisfactory series of transverse and longitudinal peel preparations. The remaining specimens, although less completely preserved, have been useful in checking structures throughout.

The seed possesses an integument with a distinctive succession of tissues, and a large basal chamber, presumably a buoyancy mechanism which aided in water transport. The only previously described seeds with which it may be compared in a general way are those assigned to Brongniart's *Codonospermum*. However, the pronounced platyspermy of the Iowa seeds, as well as the nature of the integument, seems to render necessary a new generic name.

GENERAL ORGANIZATION—

The seed has the approximate shape of a double convex lens (pl. 19, figs. 4, 5), slightly elongated in the micropyle-peduncle axis, with an extended micropyle in the form of a flattened funnel. It measures about 12 mm. in length, and in a median transverse section the major and minor axes measure 11 and 3 mm. respectively. Thus, quite different aspects are presented, depending upon whether the longitudinal section is taken through the major (fig. 5) or minor (fig. 4) axis. In order to portray clearly the various aspects of the seed two sets of diagrammatic drawings have been prepared: one, from a series of transverse sections (text-fig. 4); and the other from a series of longitudinal sections (text-fig. 5)[3] taken through the minor axis.

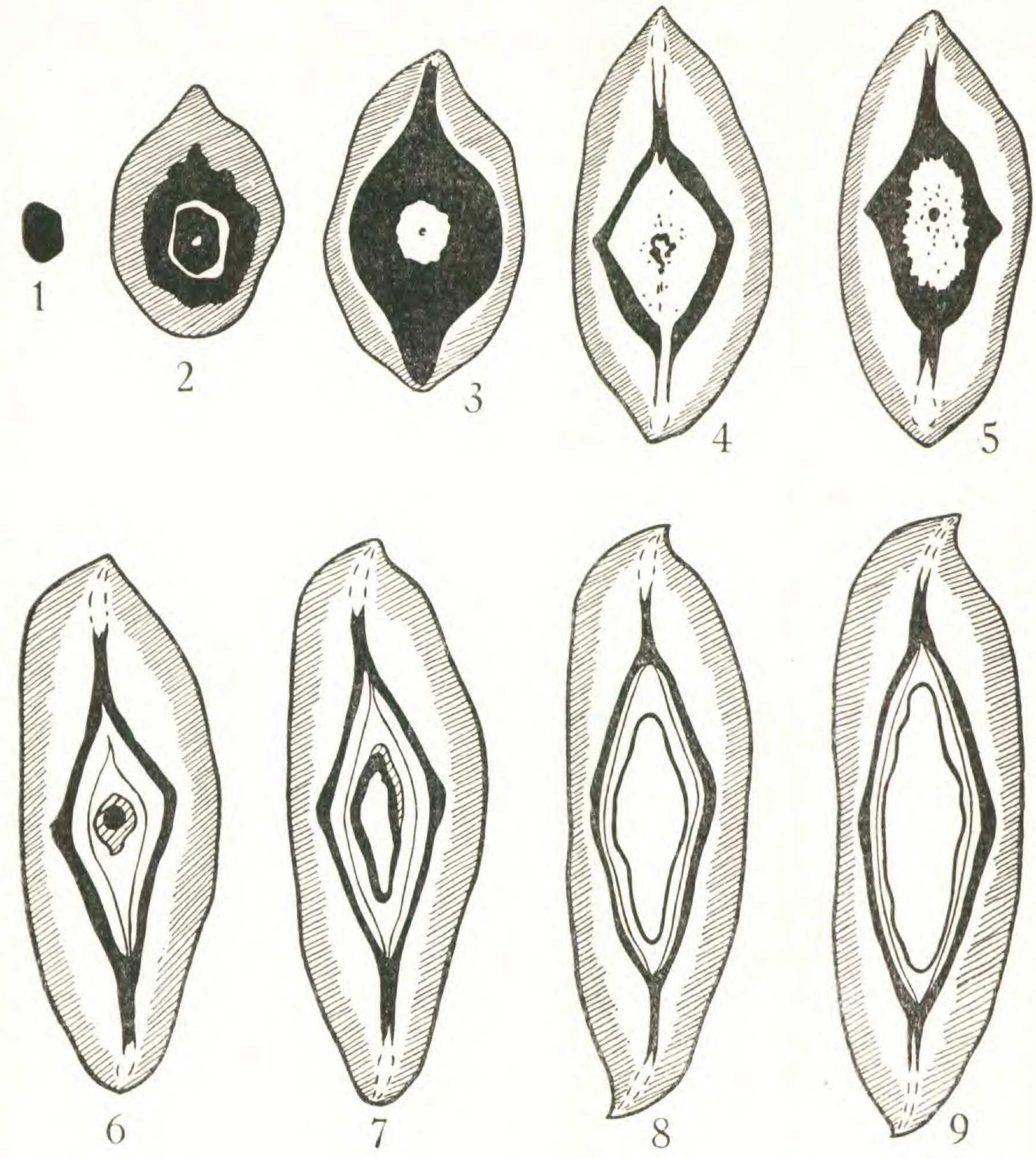
It is significant to note that the seeds, with the exception of the terminal portion of the micropyle, show no evidence of any appreciable distortion as a result of fossilization. Aside from the outer layer of the nucellus and whatever may have been within the megaspore membrane at the time the seeds were deposited, the tissues are well preserved and the gross shape as outlined in the text figures presents the true life form of the seed.

A longitudinal section (pl. 19, fig. 4, and text-fig. 3) shows that the seed is composed of two clearly defined regions: a basal chamber and nucellar chamber, with their attendant tissues. Simply as a matter of convenience these will be described separately.

NUCELLAR REGION—

Integument:—The integument is bounded externally by a single layer of epidermal cells which appear brick-shaped in both longitudinal and transverse sections. Within this epidermis is a succession of four clearly defined tissues. First

[3] All the seeds on which this description is based were contained in one small coal-ball specimen; thus it was not possible to prepare individual preparations of peels. Consequently in the longitudinal series shown in text-fig. 5 the preparations are slightly oblique, showing the micropyle or basal chamber more perfectly at one end than the other (cf. Nos. 2 and 3 with Nos. 15 and 16).



Text-fig. 4. *Kamaraspermum Leeanum.* A series of diagrammatic drawings of transverse sections extending from below the basal chamber to the top of the nucellar chamber.

1. Sclerotic tissue below basal chamber. Seed D, peel 475-T21.

2. Lowermost part of basal chamber containing prominent central vascular strand. Seed D, peel 475-T22.

3. Lower part of basal chamber. Seed D, peel 475-T23.

4. Upper part of basal chamber. Seed D, peel 475-T24.

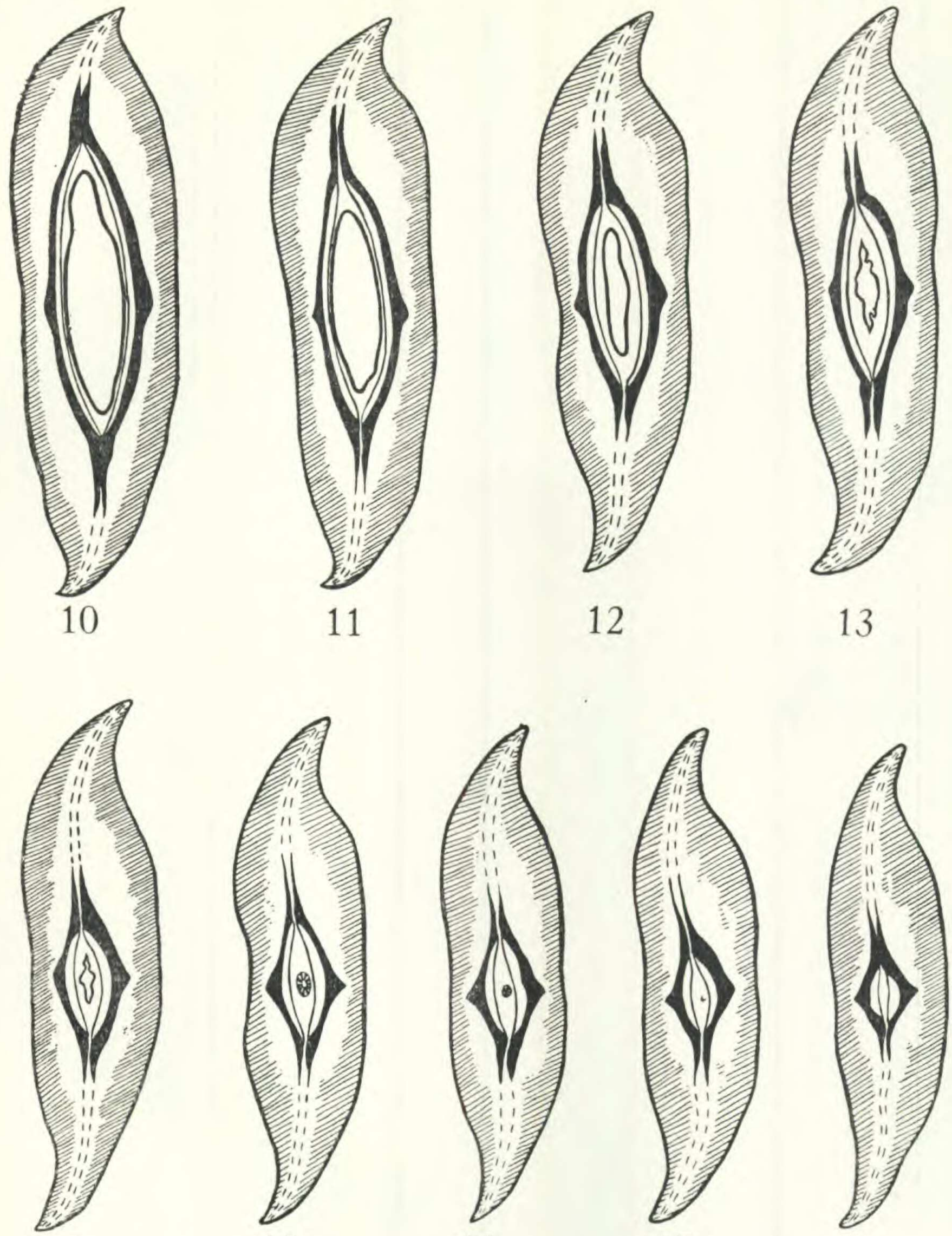
5. Top of basal chamber. Seed D, peel 475-T25.

6. Lower part of nucellar chamber, near nucellar attachment. This and the remaining figures in this series are from Seed C. Peel 475-T31.

7. Lower part of nucellar chamber. Peel 475-T30.

8. Lower third of nucellar chamber. Peel 475-T28.

9. Slightly below center of nucellar chamber. Peel 475-T26.

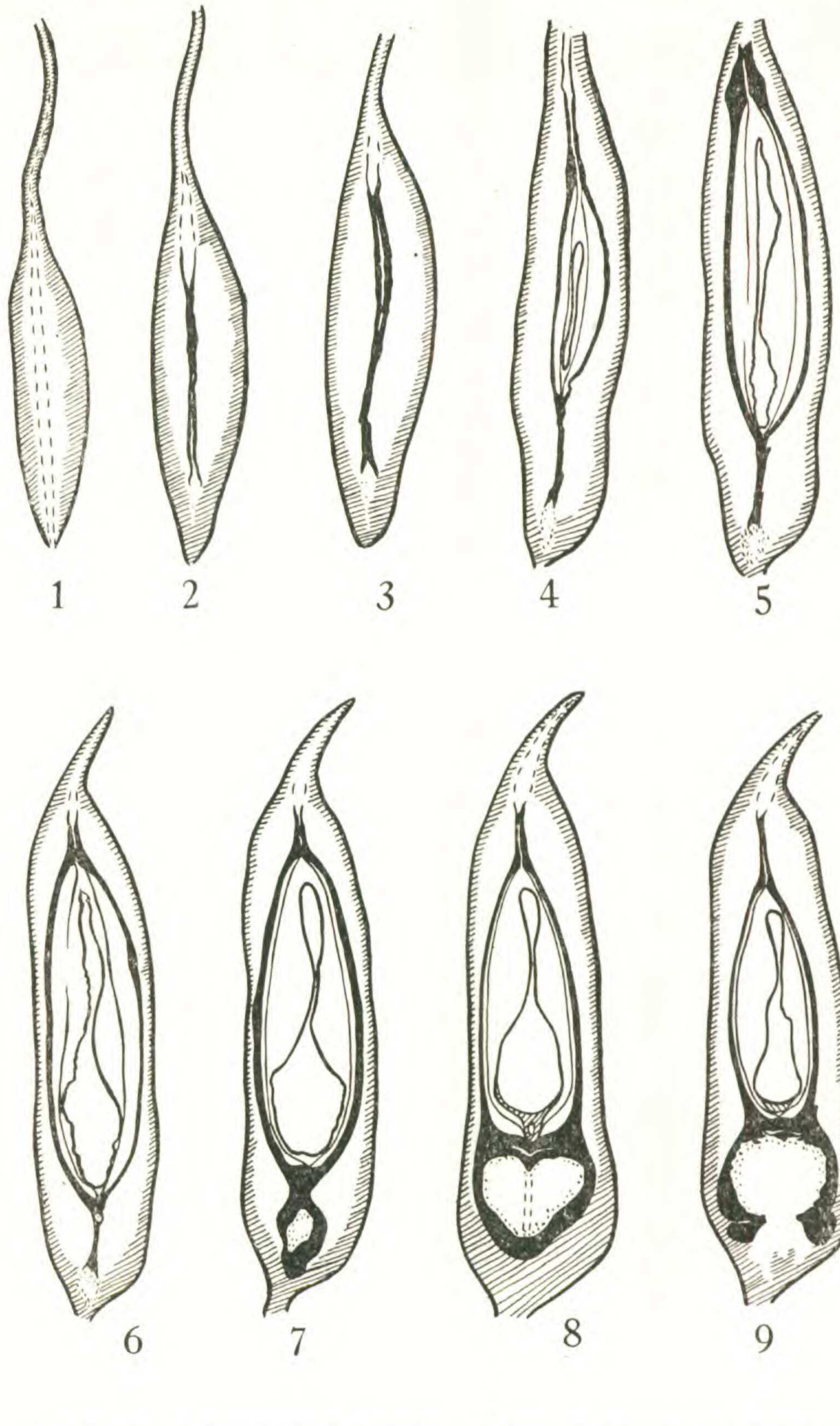


Text-fig. 4 (Continued).

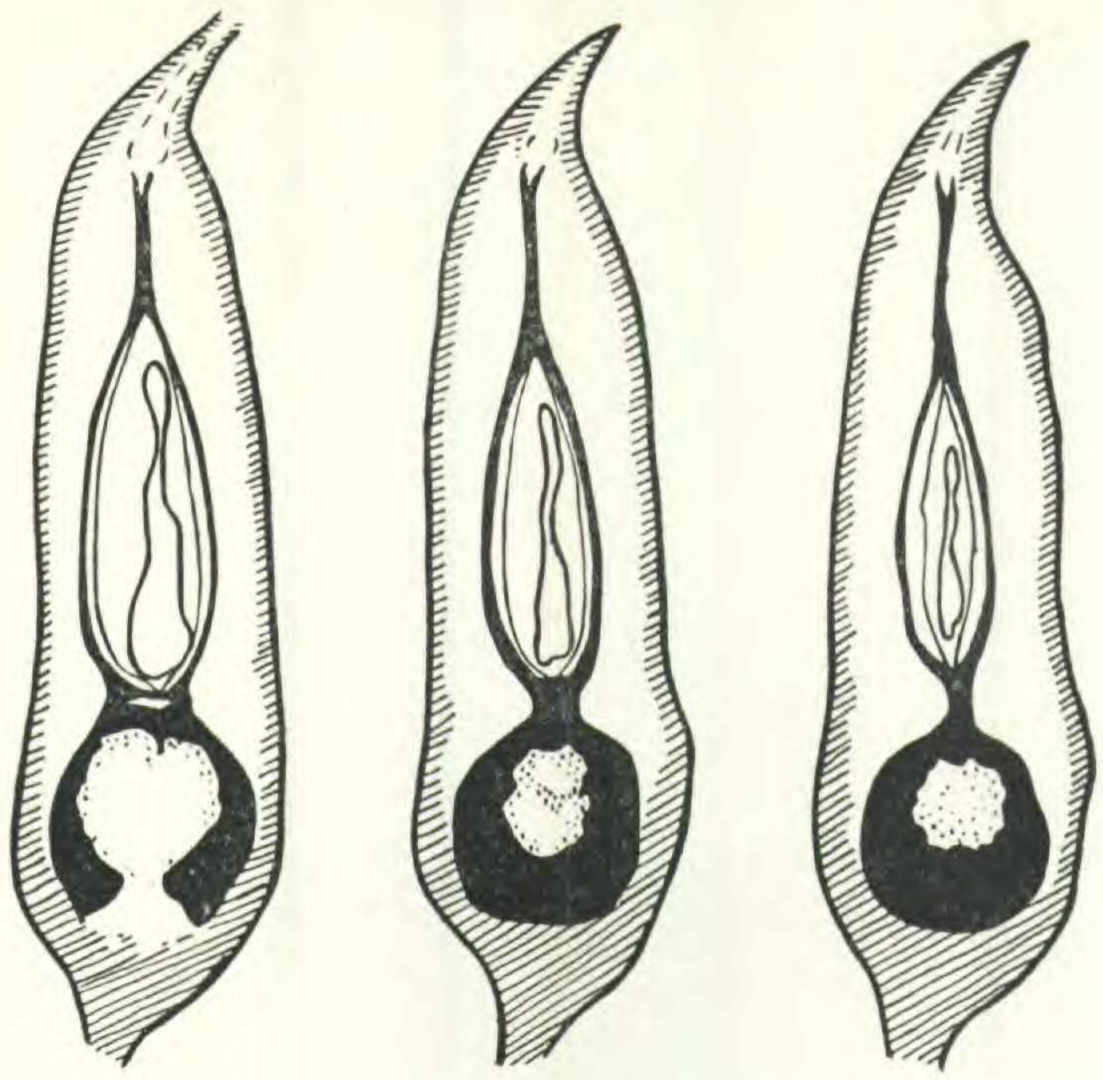
10. Slightly above center of chamber. Peel 475-T23.

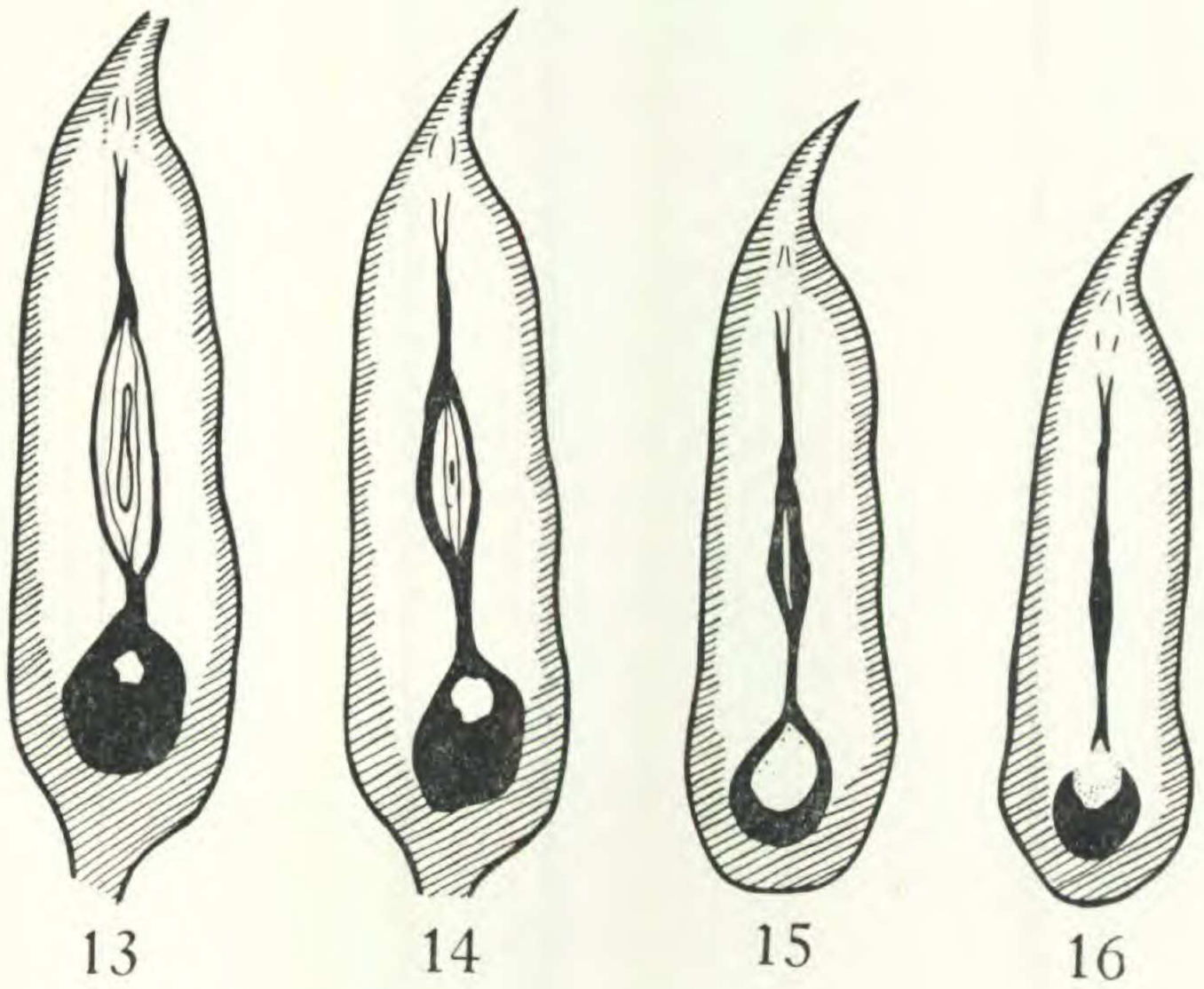
11–16. From upper part of nucellar chamber. Peels 475-T21, T19, T18, T16, T15, T12 respectively.

17, 18. Top of nucellar chamber. Peels 475-T8 and T4.



Text-fig. 5. *Kamaraspermum Leeanum*. A series of diagrammatic drawings of longitudinal sections taken parallel to the minor axis of the seed. From seed A.





Text-fig. 5. (Continued).

1, peel 475-T33; 2, T32; 3, T31; 4, T28; 5, T26; 6, T24; 7, T23; 8, T21; 9, T19; 10, T18; 11, T16; 12, T13; 13, T11; 14, T7; 15, T5; 16, T2.

is a dark-colored layer, three or four cells thick, of rather large, irregularly shaped, thick-walled cells. Within this outer sclerotic tissue is a conspicuous layer of light-colored parenchymatous cells, small and hexagonal when viewed in transverse or longitudinal section. This tissue is massive in the lower micropyle region of the integument (pl. 19, fig. 4), tapering down rather abruptly in the mid-nucellar region, and tends to become slightly thicker in the transition zone between the nucellar and basal chambers. The third layer, like the outermost one, is relatively narrow and consists of dark sclerotic cells. This expands to form a very conspicuous tissue between the nucellar and basal chambers. The fourth layer is narrow, and is composed of longitudinally elongate, brick-shaped parenchyma cells.

Micropyle:—The micropyle of *Kamaraspermum Leeanum* is a striking structure and deserving of special comment. As may be noted in the median (minor axis) longitudinal section (pl. 19, fig. 4; text-fig. 3), it consists of two quite distinct regions: a massive continuation of the integument above the nucellar chamber, and a much more slender tapering apex. These will be referred to as the proximal and distal portions respectively.

The structure of the proximal micropyle differs from that of the integument below it only in the great development of the parenchymatous (second) layer, and an absence of the innermost parenchymatous tissue. The distal portion of the micropyle is approximately 1.5 mm. long and shaped like a much-flattened inverted funnel, being twice as broad in the plane of the major longitudinal axis as in the minor axis. Like the proximal region, this portion consists of epidermis, outer sclerotic and outer parenchymatous layers, the inner sclerotic layer having terminated in the upper portion of the proximal region.

Nucellus:—The nucellus consists of the remnants of a thin layer of small brick-like parenchymatous cells surrounding the well-preserved megaspore membrane, and is attached to the rest of the seed only at the base. No pollen chamber was found in any of the seeds, although judging from what is known of petrified Pennsylvanian seeds in general, it seems likely that one did exist. If such were the case it was probably composed of delicate cells which were destroyed prior to fossilization.

Megaspore membrane:—This appears as an orange-colored band immediately within the nucellus. It becomes somewhat thicker at the base where the nucellus is attached to the integument, and sometimes a few scattered cells may be seen within the membrane.

BASAL CHAMBER—

The basal chamber consists of epidermis, outer sclerotic and outer parenchymatous tissue, each identical to and continuous with the respective layers of the integument surrounding the nucellar chamber. An inner sclerotic layer surrounds the chamber and appears to be a continuation of the inner sclerotic integument

around the nucellar chamber. This layer consists of irregular cells, which are smaller than those of the outer sclerotic layer but resemble them in shape. The inner edge of this sclerotic layer is somewhat irregular, with a few small scattered parenchymatous cells occasionally adjoining it. Although not present in the specimens at hand, a vascular strand (indicated by the dotted line in text-fig. 3) probably passed from the peduncle through the center of the chamber. Evidence for it is an area of vascular tissue visible in cross-sections at the base and at the top of the chamber. Furthermore, in one of the median longitudinal sections the chamber is strongly heart-shaped due to the extension of some sclerotic cells downward from the top of the chamber. The fact that some scattered thin-walled cells are found within the chamber suggests that it might have been occupied with a loose aerenchymatous tissue.

COMPARISON WITH OTHER SEEDS—

Kamaraspermum presents a number of structural features that render it of very great interest, yet at the same time preclude it being assigned definitely to the recognized orders of Paleozoic seeds (Seward, '17, pp. 300–365). The strong bilateral symmetry and lack of any semblance of trigonocarpous organization in transverse section seem to rule out the Trigonocarpales. In at least three important respects it diverges from characteristic Lagenostomalean seeds: *Kamaraspermum* is strongly platyspermic; the nucellus is free from the integument; and the integument as a whole is comparatively thick. Its affinities lie closer to the Cardiocarpales than either of the previous two orders, and it seems most expedient to consider it tentatively as a member of this group. The chief conflicting feature here, however, is the structure of the integument. A typical Cardiocarp seed, as the present authors understand it, has an integument with a conspicuous and bulky outer fleshy sarcotesta, while *Kamaraspermum* presents in the sequence of its integumentary tissues: first (outermost), a sclerotic layer, then a relatively fleshy layer followed by another sclerotic one.

It is also appropriate to comment briefly on the prominent basal chamber. Usually where there is a lack of tissue in a petrifaction the possibility of loss through decay exists. Yet, since the Iowa seeds are generally well preserved and a similar basal chamber occurs in the French *Codonospermum* species (Brongniart, '74, '81; Renault, '96), it appears likely that the basal chamber existed as such in life. However, since the chamber region contains some remnants of delicate tissue it may be that it was occupied by a very loosely organized aerenchyma. In either event there can be little doubt that it functioned as a float mechanism.

The possibility of Lepidocarpalean affinities has also been considered. There are certain points of similarity between *Kamaraspermum* when viewed in median longitudinal section and a tangential section of a *Lepidocarpon* taken through the "heel" or distal end of the sporophyll. The symmetry of *Kamaraspermum*, its complex integument and micropyle, nature of the remnants of the outer nucellar

tissue are, upon more critical examination, found to be in no way related to those of any described species of *Lepidocarpon.*

One is almost tempted to apply the nebulous term "missing link" to this curious fossil, with its non-conformity to established groups, yet the evidence seems to point in the direction of the Cardiocarpales, to which order it is tentatively assigned.

Diagnosis:—Kamaraspermum Leeanum: platyspermic seed 12 mm. long, 11 x 3 mm. in median transverse section; conspicuous chamber beneath nucellar region; integument composed of thin outer sclerotic layer, conspicuous fleshy layer, inner sclerotic layer, and thin inner parenchymatous tissue; micropyle of two clearly defined regions: a massive continuation of integument above nucellar chamber, and delicate distal portion shaped like a flattened funnel.

Locality: Urbandale Coal Mine, Des Moines, Iowa.

Horizon: Des Moines Series, Pennsylvanian.

Type specimen: No. WCB475, Henry Shaw School of Botany paleobotanical collections.

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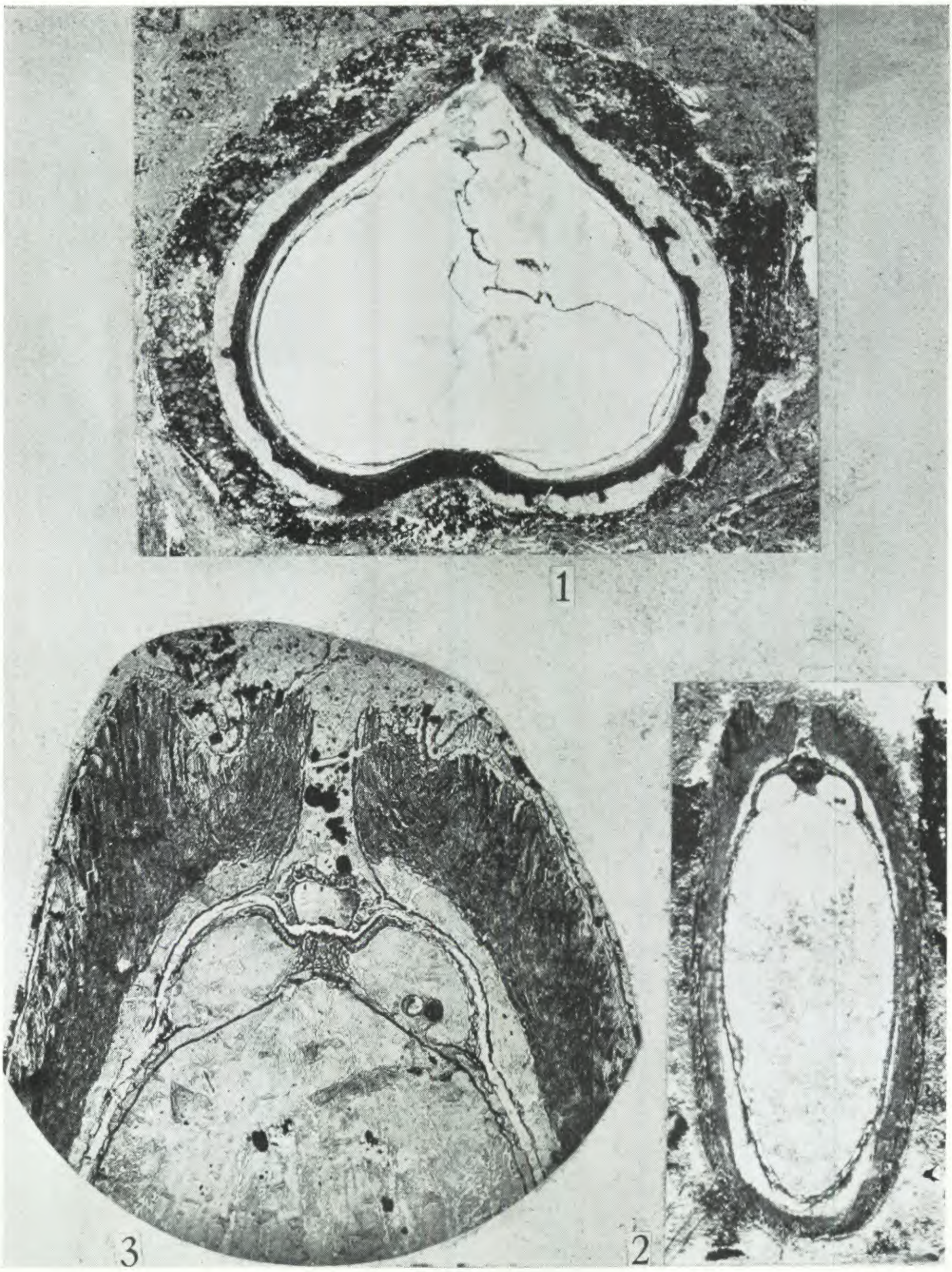
Explanation of Plate

PLATE 18

Fig. 1. *Rhabdospermum spinatum.* A nearly median longitudinal section. See text-fig. 2 for cellular structure of integument. From peel 493-T3. Magnified x 6.

Fig. 2. *Conostoma oblongum* Williamson. A nearly median longitudinal section through the seed. From slide 1398. Magnified x 13.5.

Fig. 3. The micropylar region of the seed shown in fig. 2, at a higher magnification. From slide 1398. Magnified x 41.



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EXPLANATION OF PLATE

PLATE 19

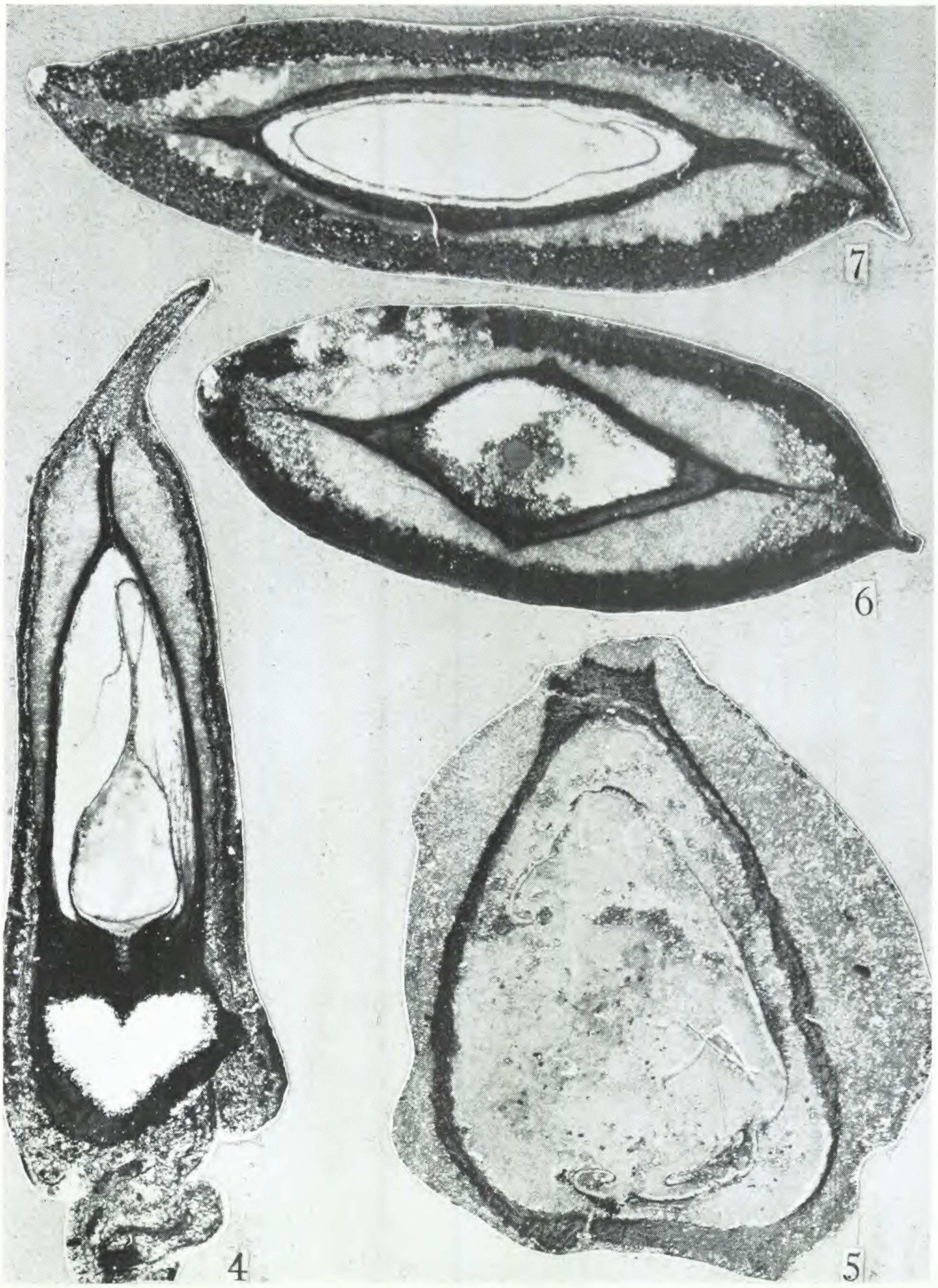
Kamaraspermum Leeanum Kern

Fig. 4. Median longitudinal section along minor axis. Seed A, peel 475-T21. x13.

Fig. 5. Longitudinal section along major axis. Peel 475-T14. x 12.

Fig. 6. Transverse section through lower part of nucellar chamber, just above point of nucellar attachment. Seed C, peel 475-T26. x 12.

Fig. 7. Transverse section through central portion of nucellar chamber. Seed C, peel 475-T23. x 12.



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